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With the advent of sensory engineering, it may be possible to circumvent the problems of spatial disorientation, increase efficiency, and/or improve performance in self motion tasks by the modification of visual information. As a first step to this end, the visual information necessary for optimal motion perception was explored. In one set of experiments, the effect of eye movements on the ability to perceive small speed or direction differences was investigated. The results indicated that the most precise speed discriminations are obtained when eye movements are minimized. This result has implications for improved motion discrimination precision in artificial or image-controlled environments. With regard to estimations of distal motion, eye movements had little effect when the retinal motion was faster than 2 deg/sec. In a separate set of experiments, the spatial frequency requirement for the perception of motion direction was determined. The results revealed a narrow band of optimal spatial frequencies sufficient for accurate path discrimination. These results have potential engineering applications. Given that a narrow band of optimal spatial frequencies is sufficient to support path discrimination indicates that image transmission efficiency can be increased without a loss in performance.

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VISUAL PERCEPTION OF SELF MOTION

AFOSR Final Technical Report

by

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1997

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CHAPTER I

INTRODUCTION

Knowing the visual stimulus requirements for self motion perception is critical for the development of solutions to the problem of spatial disorientation. With the advent of sensory engineering, and new developments in technology, it may be possible to circumvent the problems of spatial disorientation, increase efficiency, and/or improve performance in visually-related tasks by the modification of visual information. As a first step, basic science questions regarding the nature of the requisite visual information for the perception of self motion need to be addressed. To understand the role of vision in motion perception is the primary aim of the proposed research.

The influence of many factors on motion perception has been revealed from basic science research. For example, it is known that a person's ability to discriminate the direction of motion is dependent upon the speed of the stimulus as well as on its spatial frequency and contrast. However, other factors, such as a person's eye-movement pattern, have been largely unaddressed. These factors may also influence motion perception and may be modified to increase efficiency and/or improve performance.

One of the current thoughts is that the retinal effects of eye

movements can be compensated by an extra-retinal signal--that is perhaps a copy of the motor command signal to move the eyes. When the retinal and extra-retinal signals combine the observer is able to retrieve information about the distal stimulus. If this were so then whether or not a person made eye movements should not affect the accuracy of discriminating path of locomotion. On the other hand, if the compensation is incomplete then we would expect path discrimination to be less accurate under conditions of eye movement and we could improve our accuracy by not making pursuit eye movements while judging path of locomotion.

Previous studies have attempted to look at the effects of eye movements on heading judgments, and the conclusions are varied. Some of the problems with the past studies stem from the fact that eye movements were either not measured or measured imprecisely. A pursuit target was presented superimposed on a flow pattern and the subject was instructed to keep their eye fixated on the target. It was then assumed that the eye moved at the speed and in the same direction as the pursuit target. However, it has been shown that subjects rarely have accurate tracking when there is a moving background. So the interpretation of these studies may be biased and could explain the failure to achieve

consensus.

Along a different vein, much effort is currently being devoted to developing ways to reproduce images of high fidelity; images that require high information transmission rates. However, high image quality may not be necessary for successful performance on tasks such as spatial orientation. Low and high spatial frequency bands may not carry useful, or equivalently useful, information for the perception of self-motion direction. It may be that some image information in the optic flow patterns is dispensable for optimal performance. If so, a more efficient image representation for the spatial orientation task can be defined. That is, the images can be modified so as to contain only the necessary spatial frequency components. In this way, information transmission efficiency can be increased without decreasing performance. The demonstration of a optimal spatial frequency band for motion judgments would not only have implications for increased transmission efficiency but also for improving performance under low-visibility conditions. In such situations, it may be possible to increase visibility by enhancing the contrast in the critical spatial frequency band at the expense of information in the other bands without a loss in human performance. By reducing the processing load (human and machine) in the other spatial frequency bands, more resources

could be devoted to other tasks such as target recognition. Recent advances in technology have made possible the idea of modifying retinal images and they have introduced several opportunities for using modified images. For example, in flight simulators they are using simulations of real-world scenes for training purposes. Devices, such as helmet-mounted displays are being developed to aid in aircraft control and target acquisition. Possibly in the future aircraft operators might view images of the real world instead of the actual environment or there may be unmanned aircraft where control of the aircraft is done remotely via transmitted images. In any event, decisions must be made concerning what information needs to be in the images for successful performance.

In the following sections, the background and main results of several experimental studies are described. The studies were conducted to understand the role of vision in self-motion perception. Methodological details of the experiments are briefly described since they are readily accessible in published form. Experiments that investigated the perceptual effects of eye movements on motion perception are described in the first section. The studies investigated whether or not eye movements are <u>detrimental</u> to perceptual judgments of speed and

direction. Experiments that investigated the spatial frequency requirements for judgments on the direction of motion are described in the second section. The studies investigated whether there is a band of spatial frequencies that is optimal for accurate path discrimination and whether a narrow band of the optimal spatial frequencies is <u>sufficient</u> for accurate judgments of motion direction.

CHAPTER II

EFFECTS OF EYE MOVEMENTS ON MOTION PERCEPTION

Motion perception with image stabilization: Speed discrimination of sinusoidal gratings[1]

Psychophysical studies that investigate the properties of motion processing mechanisms often fail to accurately specify the stimulus. Most studies implicitly assume that the retinal image which provides input to a motion mechanism mirrors the distal stimulus. One problem with this framework is that the distal stimulus is not the only input to the retinal image; rather, retinal-image motion is the vectorial sum of the stimulus motion and the coincident eye movements.

Human observers cannot voluntarily inhibit eye movements when the visual field is composed entirely of moving targets and no fixation stimulus is provided (Kowler & McKee, 1987; Murphy, Kowler & Steinman, 1975). Psychophysicists can reduce unwanted eye movements by using a stationary fixation point (Murphy, et al., 1975); but, the fixation mark may be problematic if it introduces relative spatial cues that confound the measured behavior. Other attempts to minimize eye movements may include restricting stimulus durations to times shorter than the putative latency of smooth pursuit eye movements, approximately 150 to 200 msec, and randomly varying the direction of stimulus motion. However,

none of these procedures circumvent all eye movements. Anticipatory eye movements, which occur even when the stimulus motion direction and onset time vary randomly, are generated approximately *200 to 350 msec prior to the onset* of a moving stimulus (Kowler & McKee, 1987; Kowler & Steinman, 1979a, 1979b, 1981). Additional eye movements also can occur when an attempt is made to control movements by asking subjects to track targets moving at slow velocities. The corresponding eye movement recordings show noisy eye oscillations superimposed on smooth pursuit, with considerable variability in eye velocity (Kowler & McKee, 1987).

Given that the retinal image motion is a composite of the stimulus motion and the eye movement, a question arises as to whether eye movements affect the sensory representation for stimulus motion. One way to assess the precision of the sensory representation is to measure an observer's ability to detect small differences in the speed of moving stimuli. Such a speed discrimination task can be viewed as one of detecting the signal, defined here as the speed difference of the stimuli, in the presence of noise, defined as perturbations of the motion signal. Presumably, noise degrades the internal sensory representation and makes signal discrimination more difficult. Past studies (McKee, 1981; Orban, DeWolf & Maes, 1984; Pantle, 1978) have shown that speed

discrimination thresholds, when discussed in terms of the distal stimulus speed, decrease as a function of stimulus speed, and then asymptote for stimulus speeds of approximately 4 deg/s and higher.

Using motion discrimination to determine the characteristics of the representation, the question can be formulated as such: For motion discrimination tasks that require the subject to judge the speed of the stimulus on the display screen, does precision increase when the retinal image is stabilized against the effects of eye movements? The non-invasive technique of using a stabilized image allows the experimenter to control the spatiotemporal properties of the retinal image, so that the retinal input is equivalent to the input that would be presented to a stationary eye.

If eye movements add noise to the sensory representation, speed discrimination performance should improve under stabilized viewing, because stabilization eliminates the effects of eye movements on retinal-image velocity and reduces the eye-movement associated noise. To test the hypothesis, we systematically manipulated the stimulus (sinusoidal gratings) reference speed (0.5 to 8.0 deg/s) as we measured speed discrimination thresholds under stabilized and normal viewing conditions. In the normal viewing conditions, eye movements were

recorded and used to estimate retinal image speeds.

As Figure 1 illustrates, speed difference thresholds for the normal viewing conditions show a general decrease with increasing reference speed. Subjects, on average, required an 18% speed difference for a reference speed of 0.5 deg/s, but needed only a 7% speed difference for a reference speed of 8 deg/s. The speed discrimination thresholds obtained under normal viewing conditions are approximately the same as those reported in other speed discrimination studies using similar conditions (e.g., McKee, 1981; McKee & Welch, 1985; Orban, et al., 1984; Pantle, 1978).

The speed difference thresholds for the stabilized viewing conditions, in general, show the same trend as the thresholds obtained under the normal viewing conditions: thresholds are highest for the slowest reference speeds and lowest for the fastest reference speeds, approximately 33% and 8%, respectively. At the slowest reference speed, 0.5 deg/s, the stabilized viewing thresholds are almost two times higher than the thresholds for the normal viewing conditions for all three subjects. Discrimination performance for stabilized viewing approaches that of normal viewing when the reference speed is greater than 1.0 deg/s, with the exception of S.H. at 4.0 deg/s.

Motion duration - 500 msec

Stimulus Reference Speed (deg/s)

Weber Threshold (Delta S/S)

Stabilized Viewing
Normal Viewing

Group Means +/- 1SEM
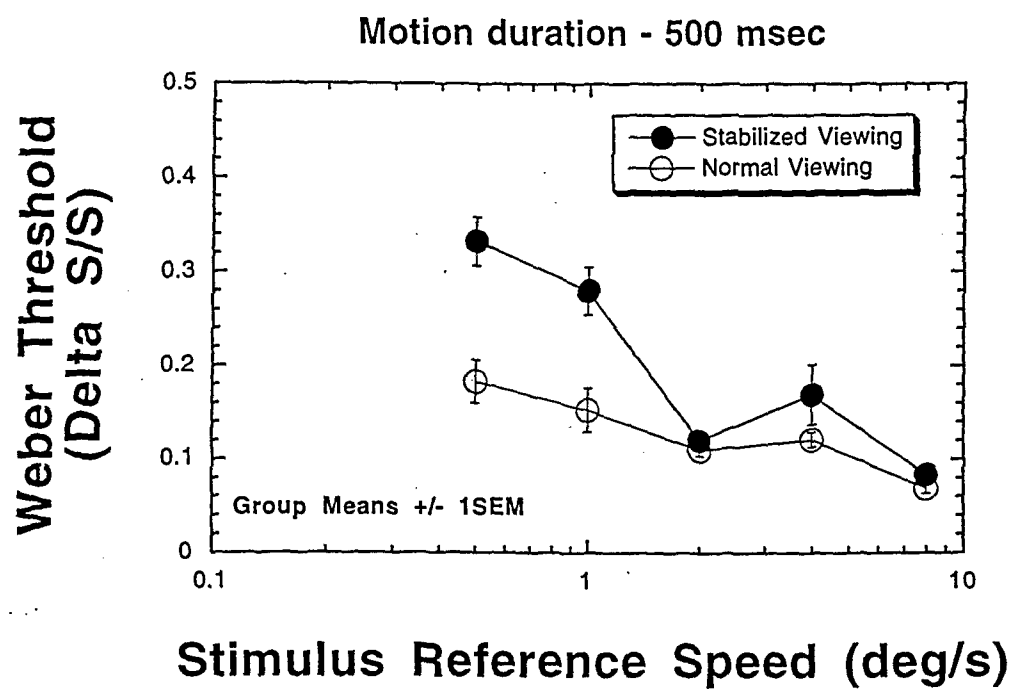
Stabilized viewing thresholds were higher than the normal viewing thresholds when analyzed in terms of distal-stimulus speed, as typically is done for studies of speed discrimination. To determine whether the difference in speed discrimination performance between the stabilized and normal viewing conditions could be explained on the basis of retinal image speed, we compared the thresholds for the two viewing conditions after adjusting for the change in retinal speeds. The retinal speed in the stabilized viewing trials closely approximates the speed of the grating on the display monitor, whereas the retinal speed in the normal viewing trials is the vectorial sum of the stimulus motion and coincident eye movements. In order to estimate the retinal speeds in the normal viewing conditions, we used the measured eye movements for two subjects that were generated while they performed the discrimination task. If speed discrimination is dependent upon the retinal-image speed, and eye movements merely alter the retinal image velocity, then thresholds plotted in terms of retinal-image speed should be comparable for the stabilized and normal viewing conditions.

Speed discrimination results obtained under normal viewing conditions are plotted in Figure 2 as a function of the average retinal speed calculated from the eye movement recordings. Here thresholds are

Figure showing two panels (KT and SH) of Retinal Speed Threshold (Delta S/ERS) versus Estimated Retinal Speed (deg/s).
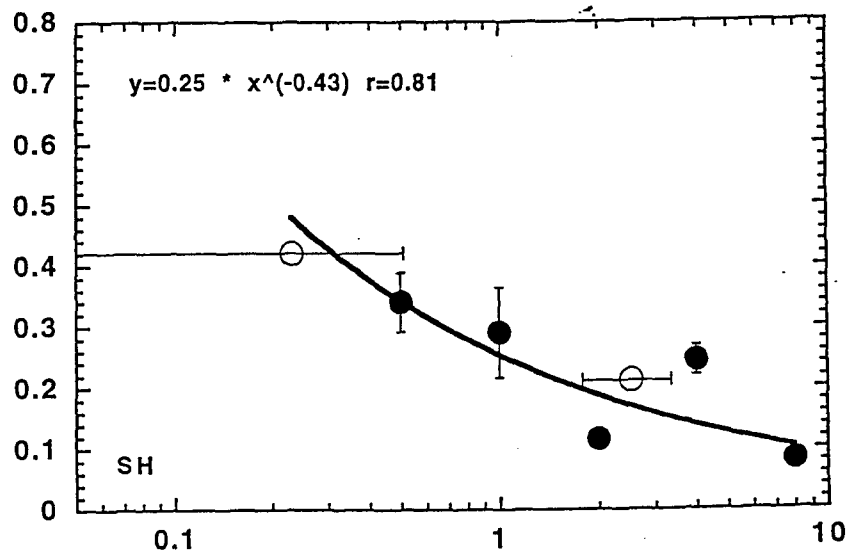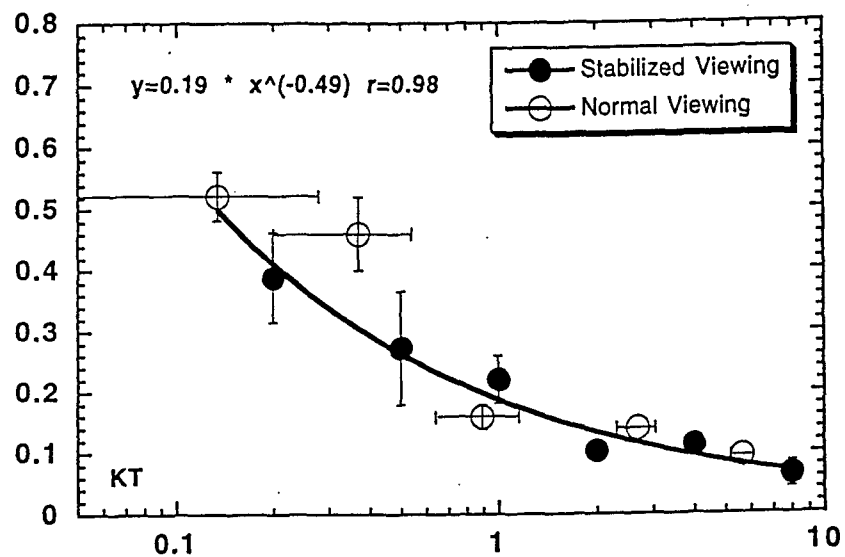
Top panel (KT): $y=0.19 * x^{(-0.49)}$ $r=0.98$
- Stabilized Viewing (filled circles)
- Normal Viewing (open circles)

Bottom panel (SH): $y=0.25 * x^{(-0.43)}$ $r=0.81$

computed as Delta S/ERS, where Delta S corresponds to the threshold delta speed and ERS refers to estimated retinal-image speed, not distal-stimulus speed. When considered within the framework of retinal speed rather than stimulus speed, the normal viewing thresholds closely match the stabilized viewing thresholds.

In summary, the results of this study show that speed discrimination thresholds, expressed as Weber ratios relative to stimulus speed, are higher when measured with image stabilization than when measured under normal viewing conditions for slow stimulus speeds. When equated in terms of retinal speed, there is no difference between the stabilized viewing and the normal viewing thresholds. A retinal-image motion model is a parsimonious explanation for the results.

Motion perception with image stabilization: Path discrimination of optic flow patterns[2]

As a person moves relative to the environment, s/he continuously judges her/his spatial orientation (e.g. direction and path of self motion) based on sensory information from the visual, vestibular, and somatosensory systems. Visual information has been shown to play a key role in the perception of self motion. Self motion transforms the pattern of light intensities reflected from objects, and this transformation, referred to as optical flow, is specific to the person's movement(Gibson, 1950). Studies have shown that people can use computer-generated patterns of optical flow to accurately judge the path and direction of the simulated self motion (Riemersma, 1981; Warren, Morris, & Kalish, 1988; Warren, Mestre, Blackwell, & Morris, 1991; Warren & Hannon, 1990; Warren & Kurtz, 1992; Royden, Banks, & Crowell, 1992; Crowell & Banks, 1993; Turano & Wang, 1994).

Optical flow can be represented as an instantaneous velocity field analyzable as the sum of a translational and rotational component. The common point of origin of the velocity vectors of the translational component is spatially coincident with the direction of self motion. Optical flow composed solely of a translational component is generated

as a person navigates a straight motion path. Curvilinear motion introduces a rotational component into the velocity field.

On the retina, the optical flow is altered by eye movements; the velocity vectors generated by eye movements sum with the rotational component in a vectorial manner. Thus, the rotational component of the retinal flow may be generated by a person moving along a curved motion path or by a person moving along a straight path making eye movements. Given that eye movements appear to interfere with the visual information specifying self motion, we questioned whether the elimination of the effects of eye movements from the retinal flow would result in more accurate judgements about self motion.

The role of eye movements in self-motion perception is a relatively new area of research, and the conclusions drawn from the few studies are in disagreement(Warren & Hannon, 1990; Royden *et al.*, 1992). In one study, Warren & Hannon (1990) investigated whether human subjects could accurately perceive the direction of self motion while making pursuit eye movements. Using computer-simulated images, subjects judged the direction of self motion as they simultaneously pursued a moving fixation point. The results showed that subjects judged heading direction as accurately when the fixation point was moving as when it

was stationary. Warren and Hannon stated that this finding demonstrated that eye movements do not hinder self-motion perception.

To determine whether extra-retinal information (e.g. proprioceptive feedback from the extraocular muscles or efference information) is necessary to compensate for the effects of eye movements, Warren and Hannon (1990) had subjects fixate a stationary point and judge heading direction using displays that simulated the optical effects of an eye movement. Ideally, the subject would not generate eye movements but the retinal image would be altered in such a way as if eye movements had been made. Improved performance in the eye-movement condition would signify the involvement of extra-retinal information. The results, which showed comparable performance in the two conditions, led Warren & Hannon to suggest that, when available, retinal information is sufficient for accurate perceptions of heading direction.

To more fully examine the effects of eye movements in self-motion perception, Royden & colleagues (1992) conducted a study similar to Warren & Hannon's but with an extended range of simulated eye velocities. As in Warren and Hannon's study, performance in the simulated condition was compared against performance in the eye-movement condition at levels where the pursuit target velocity matched the

simulated eye velocity. The data showed that, at fast eye velocities, subjects performed better when they made a real eye movement than with displays that merely simulated an eye movement. Royden & Banks interpreted the results to mean that retinal-image information is not enough to perceive accurate heading direction; extra-retinal information is needed to compensate for eye movements, at least with fast eye velocities.

A problem shared by both studies is that eye movement recordings were not made or reported. There is reason to suspect the tracking accuracy of the subjects in the two studies. In an unrelated study, it has been shown that pursuit gains (i.e. eye speed/target speed) are significantly less than 1 when subjects are required to make psychophysical judgments about moving stimuli and simultaneously pursue a moving target (Kowler & McKee, 1987). If the subjects within the Warren & Hannon or Royden et al. studies failed to achieve pursuit gains of 1, the comparisons they made would have been inappropriate. Gains less than 1 would have caused the eye speed to have been overestimated in the eye-movement condition, thus biasing the eye-movement condition over the simulated condition. Since eye movement measurements were not reported in either of the studies, there

is no way of knowing how performance in the two conditions actually compares.

In this study, path-deviation thresholds were measured as the effects of eye movements in the retinal flow were minimized through image stabilization. With image stabilization, the subject can move his/her eyes but there will be little to no retinal effects of the eye movement. Thresholds obtained with image stabilization were compared to those obtained with unstabilized viewing to determine whether the elimination of eye movements from the retinal flow improves self-motion judgments.

Angular-speed thresholds are plotted against forward speed in Figure 3. The open and closed circles represent the data obtained in the unstabilized- and stabilized-viewing conditions, respectively. In the unstabilized-viewing condition, the two subjects detected a departure from a straight path of motion when the deviation was as small as 3.5 - 5 arcmin/s at a forward speed of 2.0 m/s. At the faster forward speed of 26.4 m/s, the subjects required a larger deviation (26 - 33 arcmin/s) to discriminate between the two motion paths. In the stabilized-viewing condition, the subjects discriminated between a straight and curved motion path only when the deviation between the two paths reached a
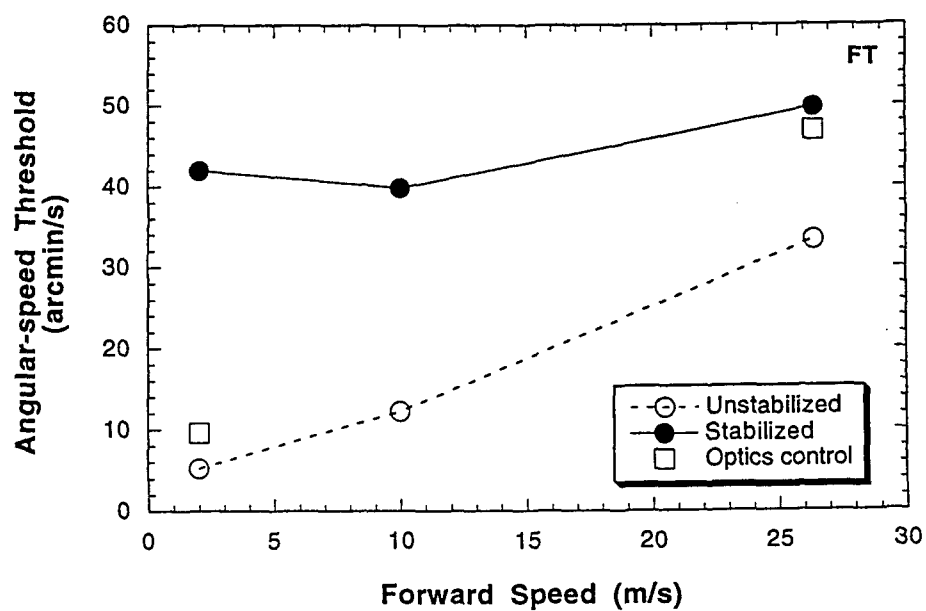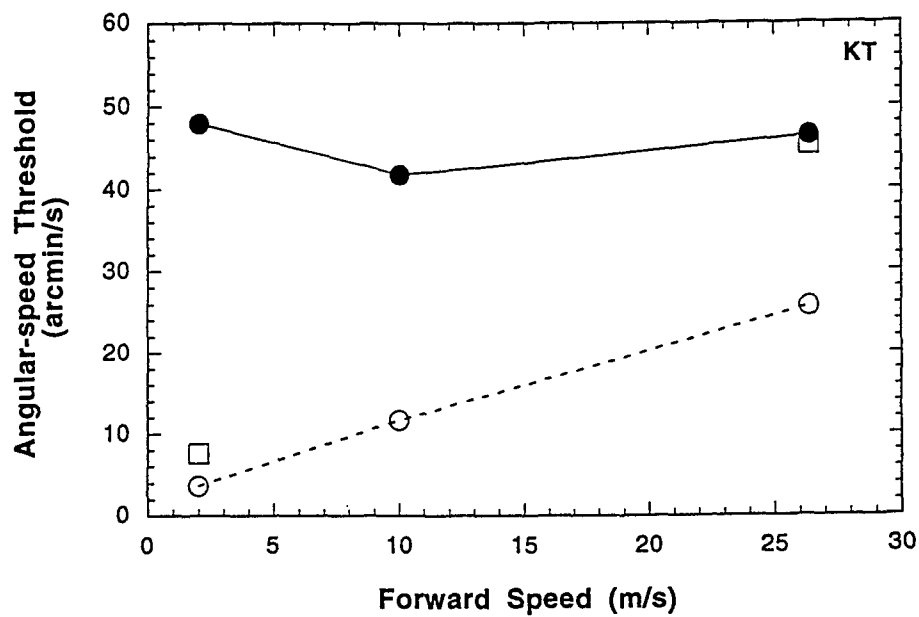
minimum angular velocity, approximately 40 -50 arcmin/s, independent of forward speed. Contrary to the expected, the elimination of the effects of eye movements from the retinal flow did not improve performance.

In an effort to understand the results in terms of retinal-image motion, eye movements were measured in unstabilized-viewing conditions, and the measured eye velocities were used to estimate the retinal-image motion. The results showed that, for slow forward speeds, eye movements increased the average retinal speed, independent of the circular flow direction. At fast forward speeds, there was no significant increase in the average retinal-image speed due to eye movements. A parsimonious explanation for the decreased performance with image stabilization at the slow forward speed is that retinal-image motion was too slow to optimally stimulate the visual motion sensors.

In summary, the present study shows that eliminating the retinal-image effects of eye movements through image stabilization can affect self-motion judgments. At slow forward speeds, subjects required more of an angular deviation to discriminate a circular from a straight motion path when the image was stabilized than when it was not. With image stabilization, subjects required a minimum angular velocity of approximately 45 arcmin/s to discriminate between a curved and straight

motion path, independent of forward speed. This value decreased to less than 9 arcmin/s at a forward speed of 2.0 m/s when the subjects viewed the display in the unstabilized conditions.

The average retinal speed for the 2.0-m/s stabilized-viewing condition was quite low, averaging between 0.15 - 0.2°/s within the central 10° and between 0.22 - 0.28°/s within the central 20°. It is possible that these low speeds were the reason that performance with image stabilization was poor. In the unstabilized viewing conditions, the measured eye movements increased the average retinal-image speed by approximately 30 - 50%.

Pasternak and Merigan (1984) measured direction difference thresholds as a function of the stimulus speed using dot patterns that translated within a plane. They found that human observers' ability to discriminate small differences in motion direction decreased linearly with decreasing speeds less than 2°/s. Specifically, subjects required approximately twice as large of a direction difference with a stimulus speed of 0.38°/s compared to 0.56°/s for accurate discrimination performance.

The relationship between direction-difference thresholds and stimulus speed, taken together with the retinal-image speed difference

in the stabilized and unstabilized viewing conditions, suggest that the retinal-image motion hypothesis for the present results is viable. The fact that image stabilization is a complex process that could involve interactions from signals of the oculomotor control system should be pointed out. But any explanation of the present results based on signals of the oculomotor control system would most likely be less parsimonious than the current one.

Motion perception during smooth pursuit eye movements: Speed discrimination of sinusoidal gratings[3]

Judgments about speed differences of objects in the world are frequently made. During these judgments, smooth pursuit eye movements occur, unless the observer is purposely maintaining fixation on a stationary target (Kowler & McKee, 1987). The smooth pursuit eye movements sum with the distal stimulus motion in a vectorial manner to produce the retinal motion. Thus, a direct consequence of eye movements is a transformation of the retinal-image motion of the distal stimulus.

Consider the retinal-motion effects of variously moving objects within a scene as a person makes smooth pursuit eye movements. Case 1, when the eye moves in the opposite direction to an object within a scene the retinal motion of that object will be faster than when the eye is stationary. Case 2, when the eye moves in the same direction as the object but at a slower speed, the retinal motion will be slower than when the eye is stationary. Case 3, when the eye moves in the same direction as the object but at a faster speed, the direction of the retinal-image motion will be opposite the eye motion as well as opposite the retinal-image motion that is produced when the eye is stationary.

Thus, the speed and direction of the retinal-image motion can be

altered by eye movements. This fact, taken together with the understanding that the retinal-image motion is processed by the visual system and used to derive decisions about the distal stimulus, suggests that eye movements may affect the precision of speed judgments about distal stimuli.

In experimental situations where eye movements are minimized, either by having subjects maintain fixation on a stationary mark (McKee, 1981; Orban, de Wolf, & Maes, 1984; Pantle, 1978) or with image stabilization (Heidenreich & Turano, 1996), retinal speed closely matches the distal-stimulus speed. Under these conditions, speed-discrimination thresholds for reference speeds up to 16 °/s asymptoted at approximately 5 - 10% of the reference speed.

In this study, the hypothesis that smooth pursuit eye movements affect speed-discrimination thresholds in a manner consistent with the transformed retinal speed was evaluated. Subjects judged speed differences of sine-wave gratings while they simultaneously pursued a superimposed moving bar. Speed-discrimination thresholds were measured under conditions of controlled eye movements, for grating speeds of 0.5 and 2.0 °/s across a range of eye velocities. Speed-discrimination thresholds were simulated using a Monte Carlo method

based on the retinal-motion hypothesis, and the simulation predictions were compared to the psychophysical results.

In Figure 4, speed-discrimination thresholds are plotted as a function of the average eye velocities. (Retinal velocity is denoted on the upper x axis.) The left- and right-side graphs represent the psychophysical data and the Monte Carlo simulation results for the 0.5-°/s and 2.0-°/s gratings, respectively. Psychophysical data are shown as symbols, and the simulation results are shown as thick lines (solid lines represent results obtained with variable eye velocity and dashed lines represent results obtained with fixed eye velocities). The dotted lines indicate the threshold levels obtained when no pursuit stimulus was present.

If eye movements have no effect on speed-discrimination performance, then the data should fall on a horizontal line whose y-intercept equals the threshold for a 0-°/s eye velocity. If eye movements have an effect on speed-discrimination performance and the effect is totally explainable in terms of retinal-image motion, then the data should fall near the model predictions, with about as much variability as is shown by the simulation results. As shown, the data do not totally comply with either of these two predictions.

Retinal Velocity (deg/sec)
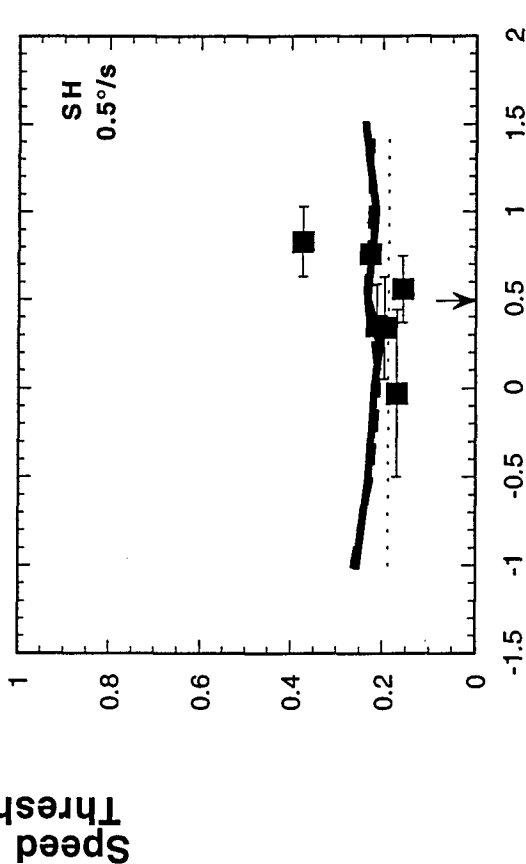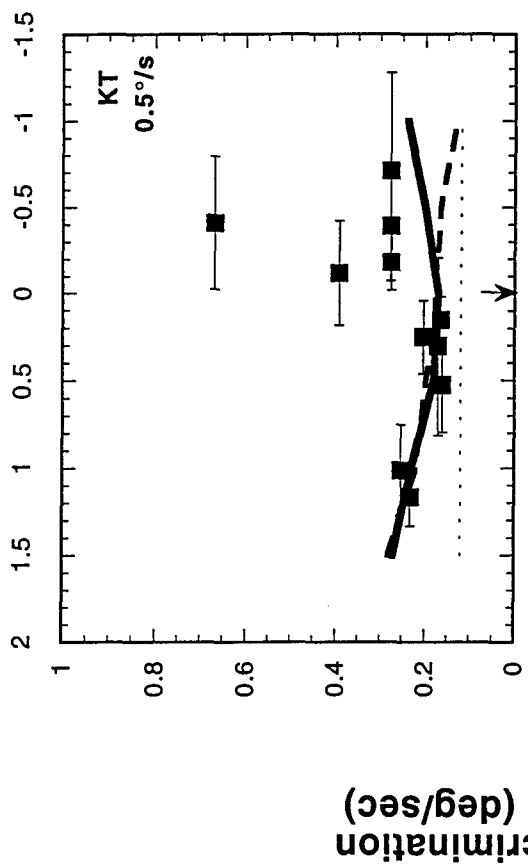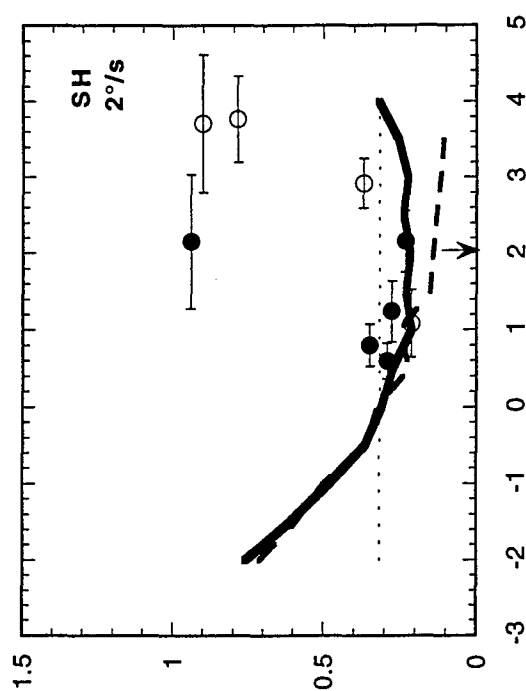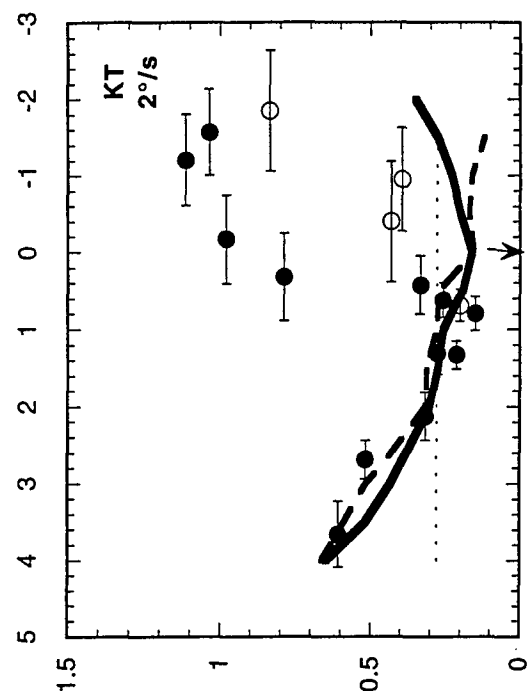
Average Eye Velocity (deg/sec)

Speed Discrimination Threshold (deg/sec)

KT
2°/s

SH
2°/s

KT
0.5°/s

SH
0.5°/s

When the eye moves in the opposite direction to the grating (Case 1), thresholds increase with increasing eye velocity. Psychophysical data in this range closely match the simulation predictions (average mean square error of 0.003), supporting the retinal-motion hypothesis. When the eye moves in the same direction as the grating, and at a slower speed (Case 2), thresholds either remain fairly constant (0.5°/s conditions) or they decrease slightly (2.0°/s conditions). The psychophysical data in this range also match the simulation predictions reasonably well (average mean square error of 0.002). However, when the eye moves faster than the grating, in the same direction (Case 3), thresholds are significantly elevated. In this range, there is a large discrepancy between the psychophysical data and the simulation predictions (average mean square error of 0.086).

The present study demonstrates that pursuit eye movements can affect an observer's ability to detect small differences in the speed of distal stimuli. The critical factor does not appear to be eye speed, per se, but rather eye velocity relative to the distal stimulus velocity. To illustrate, speed discrimination for a 2.0-°/s distal stimulus is little affected by a 1-°/s eye movement in the same direction. However, the same eye velocity results in a threshold doubling when the distal

stimulus moves at 0.5 °/s.

The results of a Monte Carlo simulation indicate that the speed-discrimination thresholds can, in certain cases, be attributed to the transformation of retinal-image speed that occurs with eye movements. Speed discrimination performance depends upon the speed of the retinal image, and eye movements alter the retinal-image speed. Thus it is reasonable to expect that speed discrimination performance will be affected by eye movements. In Case 1, where the eye moves in the opposite direction to the distal stimulus, and in Case 2, where the eye moves in the same direction as the distal stimulus but at a slower speed, the predictions generated by a Monte Carlo simulation based on the retinal-motion hypothesis closely match the psychophysical data. In Cases 1 & 2, distal stimulus motion and eye motion have equal effects on speed discrimination performance. This is reminiscent of Murphy's (Murphy, 1978) finding that externally imposed and self-imposed retinal image motions have equal effects on contrast detection.

However, transformed retinal speed cannot account for the elevated thresholds measured when the eye moves faster than the distal stimulus, in the same direction. Some other factor is needed to account for the Case 3 results. It may be that the extra-retinal signal interferes with the

retinal-motion signals for speed judgments.

Motion perception during smooth pursuit eye movements: Speed matching of sinusoidal gratings[4]

Within our field of view, objects move in various directions at various speeds. Depending upon the saliency of the visual information and the task at hand, eyes pursue or track one of the many moving objects. In doing so, the motion of that object, as well as the motion of the other moving objects, and the visual scene in general, are altered in the image on our retinas.

Smooth pursuit eye movements add a constant displacement to the visual scene. That is, the motion vectors for the distal stimulus and the eye movement are added. Since it is the retinal image that is processed by the visual system for subsequent perceptual decisions, the effects of the eye movements on the retinal image must be compensated for in order to recover the real world motion.

To recover the real-world motion, the perceptual system must have information about the movement of the eyes. As far back as the mid 1800's, it was proposed that the human observer can compensate for changes in retinal-image motion caused by eye movements by incorporating an extraretinal signal that carries information about those movements (Helmholtz, 1962). Presumably, the extraretinal signal is

compared to the retinal-motion signal to discount the effects of the eye movements and thereby recover the true object motion.

The *distal-motion model* assumes that the effects of eye movements can be fully compensated, and therefore the perceived motion of a stimulus should be the same whether the eye is stationary or moving. According to this model, perceived speed, *P*, obeys a vector summation rule of the retinal, S_R, and extraretinal, S_{eye}, signals (Eq. 1). When the angle, θ, between the retinal and the extraretinal signals is 0, the cosine of θ is 1, and the perceived speed is determined by the sum of the retinal signal squared and the extraretinal signal squared plus twice the product of the retinal and extraretinal signals. However, when the angle between the retinal and the extraretinal signals is 180 deg, the cosine of θ is -1, and the perceived speed is determined by the sum of the squared signals minus twice the product of the retinal and extraretinal signals.

(Eq.1)

$$P = \sqrt{S_R^2 + S_{eye}^2 + 2\cos\theta\, S_R\, S_{eye}}$$

In contrast, the *retinal-motion model* assumes that there is no compensation for the retinal effects of the eye movements, and therefore observers should make perceptual judgments of the real-world motion

only on the basis of the retinal-image motion.

Several studies have investigated the perception of motion in the presence of pursuit eye movements and have reached various conclusions (Brenner & van den Berg, 1994; Freeman, Crowell & Banks, 1996; Pola & Wyatt, 1989; Royden, Banks & Crowell, 1992; Royden, Crowell & Banks, 1994; Warren & Hannon, 1990; Wertheim, 1981; Wertheim, 1994). Some studies have concluded that eye movements do not affect the perception of motion (Royden et al., 1992; Royden et al., 1994; Warren & Hannon, 1990), whereas other studies have demonstrated that, at least in some situations, eye movements do affect motion perception (Brenner & van den Berg, 1994; Freeman et al., 1996; Pola & Wyatt, 1989; Turano & Heidenreich, 1996; Wertheim, 1981; Wertheim, 1994).

One prevailing view is that the perception of motion is based on an internal representation that consists of retinal and extraretinal signals (Brenner & van den Berg, 1994; Pola & Wyatt, 1989; Turano & Heidenreich, 1996; Wertheim, 1981; Wertheim, 1994). However, other findings suggest that under certain conditions, the only information used to judge object motion is the retinal-image motion (Brenner & van den Berg, 1994; Turano & Heidenreich, 1996). Turano & Heidenreich (1996) found that changes in retinal-image motion due to eye movements can account for the elevated

speed-discrimination thresholds that result when the eyes move either in the direction opposite to the stimulus motion or in the same direction, but at a slower speed. Evidence also indicated that under different conditions, some factor other than retinal-image motion is involved. When the eyes move faster than the distal stimulus, speed discrimination thresholds are higher than predicted on retinal-image motion alone.

In this study the distal-motion model and the retinal-motion model were tested in a speed-matching experiment. It was determined whether the perceived speed of a moving stimulus viewed with a moving eye is the same as the perceived speed of the same stimulus viewed with a stationary eye. A perceptual-matching task was used to estimate a threshold point on the psychometric function that anchors the function (i.e., the point of subjective equality); this differs from discrimination measures that reflect the slope of the psychometric function. In effect, the perceptual-matching threshold indicates the speed of a test stimulus viewed while making pursuit eye movements that appears to be equal to the speed of a standard stimulus viewed while fixating a stationary point.

In Fig. 5, the speed of the test grating that appears equal to the speed of the standard speed (i.e. speed match) is plotted as a function of

the eye velocity. Positive and negative values of eye velocity indicate eye movements in the same and opposite direction as that of the grating, respectively. The speed of the standard stimulus is indicated by a star on the x axis. The predictions for the retinal-motion and distal-motion (vector summation) models are presented as solid and dashed lines in Figure 5. According to the retinal-motion model, speed match should vary in proportion to eye velocity because, to equate the perceived speeds of the standard and test gratings, the speed of the test grating needs to be adjusted by an amount equivalent to the eye velocity. According to the distal-motion model, speed match should equal the standard speed regardless of the eye velocity.

The symbols in Figure 5 represent the three subjects' speed match data. The eye velocity is the mean eye velocity calculated during the first interval, averaged over all the trials in a session. The standard deviation of the eye velocities over all the trials within the session serves as a measure of the eye-velocity variability. As shown, the data do not fully support either of the models. For some eye movements, particularly those in the opposite direction to the stimulus (shaded area in Fig. 5), the speed match approximates the standard speed; the data aligned more closely with the prediction of the distal-motion model. However, for other eye
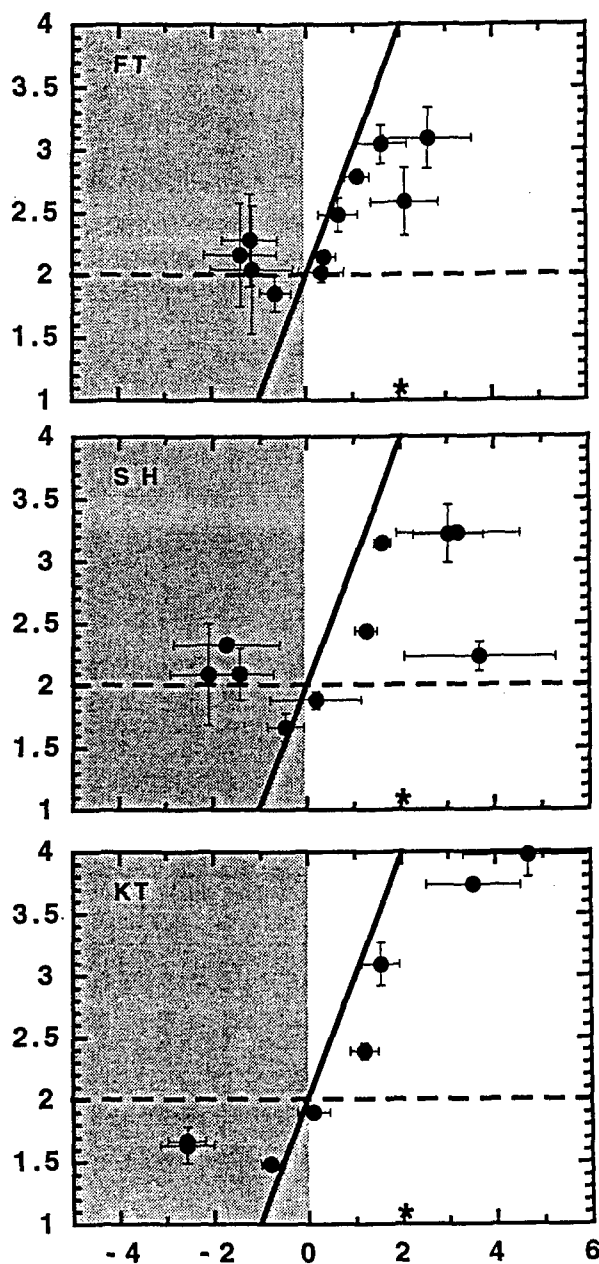
movements, this was not the case. When the eye moved in the same direction as the stimulus, but at a slower speed, the speed match increased with increasing eye speed, supporting the retinal-motion model. But when the eye moved faster than the stimulus in the same direction, speed matches did not agree with the prediction of the retinal-motion model.

The results demonstrate that eye movements can affect the perceived speed of distal stimuli. An eye movement of only 1 deg/s in the same direction as a 2 deg/s distal stimulus can decrease its perceived speed by as much as 25% of its actual speed (0.5 deg/s) when compared to its perceived speed when viewed with a stationary eye. However, the effects of eye movements on the perceived speed of distal stimuli are not determined by eye speed alone. The results show an asymmetry in the speed match errors with respect to the relative direction of eye and distal motion. An eye movement of 1.5 deg/s in the opposite direction of the distal motion produces a speed match error less than 0.3 deg/s, whereas a 1.5 deg/s eye movement in the same direction produces an error greater than 1 deg/s. Note that in Fig. 5 the largest speed match errors are made when the eye moves in the same direction as the *distal stimulus* (non-shaded area).

It is possible that the asymmetry in the results could be the direct result of the retinal-image speed. Eye movements in the same direction as a distal stimulus, and slower, reduce the speed of the retinal-image motion of a distal stimulus, whereas eye movements in the opposite direction of a distal stimulus increase the speed of the retinal-image motion. It may be that vector summation of the retinal and extraretinal signals occurs only when the retinal-image motion exceeds a minimum speed.

In Figure 6 the three subjects' speed-match data are replotted as a function of the initial retinal-image velocity of the test grating. Positive and negative values of retinal-image velocity indicate retinal motion in the same and opposite direction to that of the distal motion, respectively. Hatched areas represent retinal-image speeds faster than 1.5 deg/s. Superimposed on the data are the predictions of the two models mentioned above, the retinal-motion (solid line) and the distal-motion (dashed line) models, as well as the prediction of a third model, the eye-speed model (dotted line). The eye-speed model states that the perceived speed of the test grating will match the perceived speed of the standard grating when the speed of the test grating is equivalent to the speed of the eye movement.
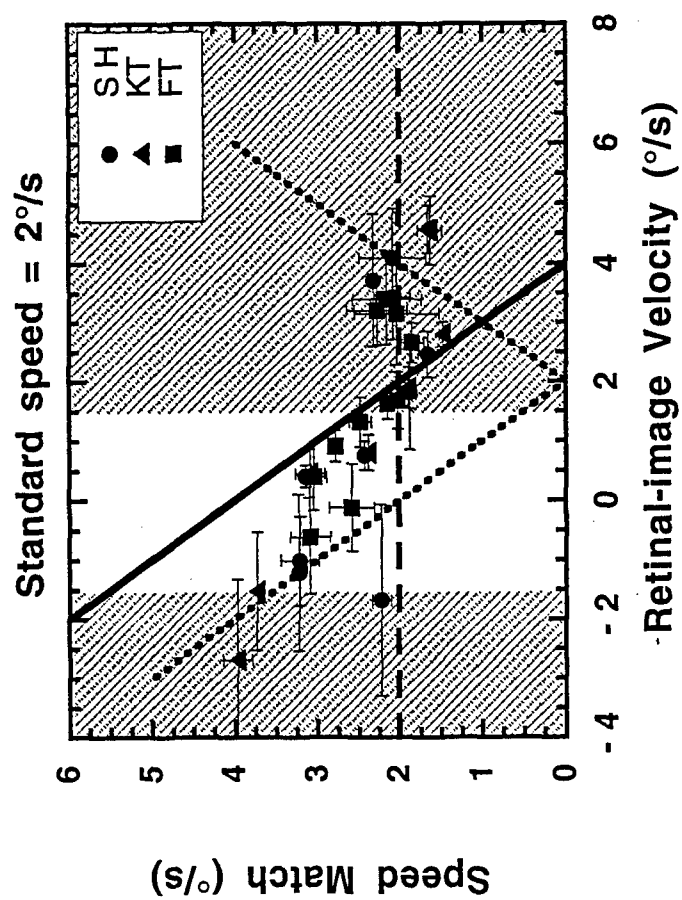
As shown, for retinal-image velocities faster than 1.5 deg/s, speed matches were fairly accurate; the subjects' data aligned reasonably well with the prediction of the distal-motion model. However, for retinal-image velocities slower than 1.5 deg/s, speed matches were inaccurate. For retinal-image motion slower than 1.5 deg/s, in the same direction as the distal motion, subjects appeared to match the retinal-image speeds of the standard and test gratings. But for retinal-image motion slower than 1.5 deg/s, in the opposite direction to the distal stimuli, subjects appeared to match the *test grating* to the speed of the *eye movement*. That is, subjects adjusted the speed of the test grating to a point where the negative retinal-image velocity of the test grating was nulled.

In the course of this study, two classical models, the retinal- and distal-motion models, were tested and, in their purest forms, rejected. The retinal-motion model, which states that a perceptual match in speed is obtained when the retinal motions are equivalent, failed to account for the majority of the data in conditions where the eye moved in the opposite direction to that of the stimulus. The retinal-motion model also failed to account for the data when the eye moved in the same direction as the stimulus but at a faster speed. The distal-motion model, which

states that a perceptual match in speed will be obtained regardless of

the motion of the eyes, failed to account for the majority of the data

obtained in conditions where the eyes moved in the same direction as, and

slower than, the stimulus.

Two hypotheses that define the conditions for eye-movement

compensation were introduced: The relative-motion-direction hypothesis

which states that compensation of the retinal effects of eye movements

occurs when the eyes move in the opposite direction to the distal

stimulus, and the minimum retinal-speed hypothesis which states that a

minimum retinal-image speed ~ 1.5 deg/s is required for the retinal

effects of the eye movements to be compensated. Both hypotheses were

supported by the data obtained with the 2.0 deg/s standard speed.

However, the minimum retinal-speed hypothesis was better supported by

data obtained with a 4.0 deg/s standard speed. Eye movements as large as

1 - 2 deg/s, in the same direction as the stimulus, generated accurate

speed matches for the 4.0 deg/s standard stimulus. This finding cannot be

reconciled with the relative-direction-of-motion hypothesis.

Both hypotheses failed to account for the increased speed match

errors at high negative eye velocities (high positive retinal-image

velocities) with the 4.0 deg/s standard stimulus. It is highly probable

that the elevated errors in this regime are due to the effects of high temporal frequency. Eyes moving in the opposite direction to a distal stimulus will increase the retinal motion of the stimulus by an amount equivalent to the magnitude of the eye motion. The coupling of fast eye speeds and fast distal motion can produce rather high temporal frequencies, which affect motion perception. For eye velocities of -2 deg/s and -4 deg/s, the corresponding retinal-image velocities are 6 and 8 deg/s. The temporal frequencies of these speeds are 18 and 24 c/sec, given a spatial frequency of 3 c/deg. In these conditions, the subjects reported difficulty in matching the test and standard speeds, claiming that the motion appeared qualitatively different.

In summary, the results demonstrate that eye movements can affect the perceived speed of distal stimuli. However, a moving eye does not always result in a misperception of distal stimulus speed. The magnitude of the speed match error is not determined by eye speed, alone, but appears to be rather by the relationship between eye and distal stimulus velocity. Neither the retinal-motion model nor the distal-motion model could explain the pattern of results. The retinal-image velocity appears to be an important factor governing which model applies. In general, for retinal-image speeds faster than 1.5 deg/s, speed matches follow the

prediction of the distal-motion model, that is, the retinal and extraretinal signals obey the vector summation rule. For retinal-image speeds slower than 1.5 deg/s, speed matches appear to follow the predictions of the retinal-motion or the eye-speed models, depending on which of the two signals (retinal or extraretinal) is dominant.

Motion perception during smooth pursuit eye movements: Direction

matching of two-dimensional uniform motion[5]

The effect of eye movements on direction perception was assessed

in a manner similar to that for speed perception. A pursue-fixate

procedure was used. The subject was presented with two motion

sequences of translating dots. The standard direction of 200 deg was

always presented in the second interval. One of five pre-selected test

directions (180 deg to -180 deg) was presented in the first interval. The

subject's task was to judge which of the two intervals the translating

dots moved more vertically. The subject was instructed to pursue (or

track) a superimposed translating bar in the first interval and then fixate

the stationary point in the second interval. There was a 1-sec interval

between the two motion sequences to allow the subject to switch from

pursuit to fixate.

In Figure 7, the perceptual matches, or PSE, are plotted against the

relative direction of the eye movement. The solid line at 200 deg denotes

the direction of the distal stimulus, and points that fall on this line

indicate accurate distal-stimulus matches. For relative directions of 0

deg and 180 deg, perception matches the distal stimulus. However, as the

relative direction of the eye movement departs from
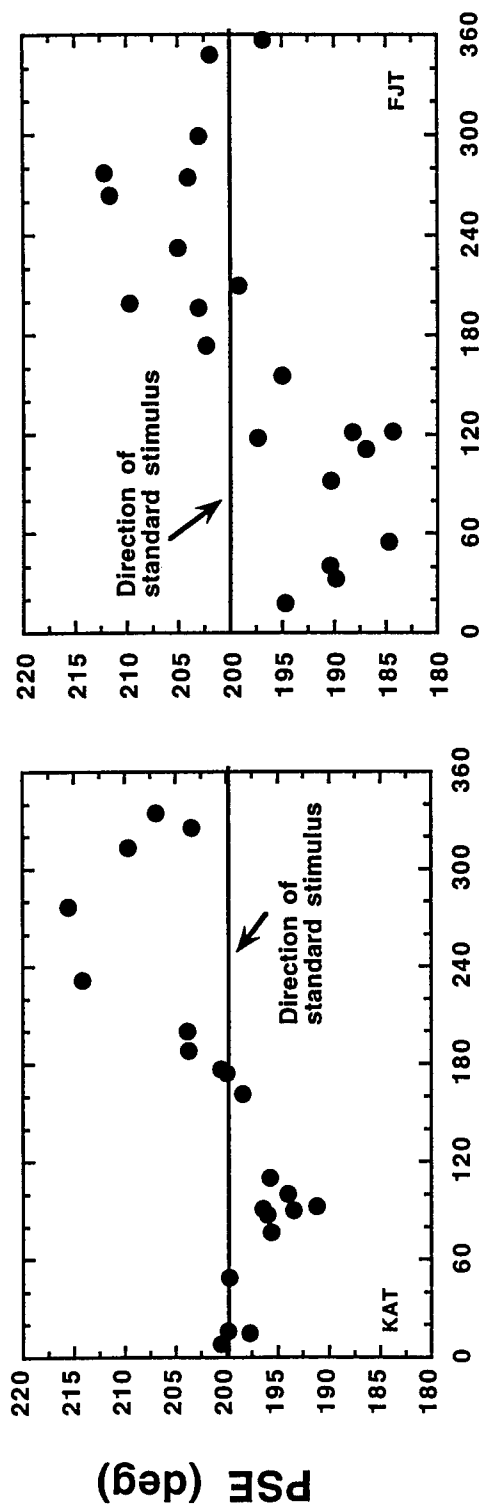
Relative Direction (deg)
(Stimulus direction - eye movement direction)

these values, the distal stimulus is not accurately matched. Deviations as large as 16 deg occur for eye movements orthogonal to the standard stimulus. Note the relationship between the perceptual match and the retinal and distal predictions. The PSE and retinal and distal predictions are similar when the eye moves in the same direction as the standard stimulus. In this case, there is no need to postulate the involvement of an extraretinal signal to achieve an accurate direction match. However, when the eye moves in a direction opposite the standard stimulus, perception does not follow the retinal prediction, instead it follows the distal prediction. In this case, it appears as if there is an extra-retinal signal that contributes to the perception of the distal stimulus motion. For relative eye movements between these two extremes, the PSE does not typically follow the retinal or distal predictions. The perceptual match is somewhere between the two, as if there were incomplete compensation of the eye movement.

CHAPTER III

SPATIAL FREQUENCY TUNING FOR DIRECTION DISCRIMINATION

<u>Optimal spatial frequencies: Spatial tuning function of optic flow[6]</u>

Human observers have remarkable accuracy in the estimation of
heading direction using only the changing pattern of light intensities
reflected from objects (Warren & Hannon, 1988; Warren, Morris, &
Kalish, 1988; Warren & Hannon, 1990). The changing pattern of light
intensities that is generated as a person moves relative to his/her
surround is referred to as optic flow (Gibson, 1950). Optic flow patterns
composed merely of random dots, rather than identifiable objects, can
support heading discrimination as precise as 1 deg for straight motion
paths (Warren & Hannon, 1988) and 2 deg for curved motion paths
(Warren, Mestre, Blackwell, & Morris, 1991). Optic flow patterns can also
support the perception of small changes in heading direction
(Riemersma, 1981; Turano & Wang, 1994).

In some of the biologically-feasible, computational models of self
motion perception it is assumed that the outputs of the
directionally-selective mechanisms, thought to underlie the perception
of two-dimensional planar motion, provide the inputs to the
three-dimensional optic-flow computations (Lappe & Rauschecker, 1993;
Perrone, 1992; Perrone & Stone, 1994; Warren & Saunders, 1995). On the

front end of these directionally-selective mechanisms are spatial and temporal filters that selectively pass information that falls within their frequency range (Anderson & Burr, 1985; Anderson & Burr, 1987; Anderson & Burr, 1989; Anderson, Burr, & Morrone, 1991; Watson & Turano, 1995; Wilson, 1985). The results of contrast-sensitivity, masking and subthreshold summation studies indicate that the spatial frequency tuning of the directionally-selective mechanisms is relatively narrow (Anderson & Burr, 1985; Anderson & Burr, 1989; Wilson, 1985), and the peak of the spatial-frequency tuning function varies in an inverse manner with stimulus speed (Kelly, 1979; Wilson, 1985). The peak of the contrast sensitivity function for the detection of a moving grating (3 deg/s) is 1.5 c/deg (Kelly, 1979). A recent study showed that the spatial frequency that which requires the least amount of contrast energy for the discrimination of motion direction is between 2-4 c/deg (Watson & Turano, 1995).

If optic flow is computed from the outputs of these directionally-selective mechanisms, we would expect the processing of optic flow to be constrained by the operating limits of the mechanisms. Furthermore, if the directionally-selective mechanisms underlie the processing of both planar motion and optic flow, then we would expect to

find similar spatial-frequency tuning for the two types of motion.

Given that optic flow generates multiple retinal speeds, the spatial frequency tuning obtained with optic flow patterns may not be as narrow as that for a single-speed planar motion pattern. On the other hand, it may be that the spatial frequency tuning of optic flow patterns will be governed by some statistical property of the retinal-speed distribution, e.g. the mode, mean, or maximum of the retinal speeds.

The spatial frequency tuning for the discrimination of small direction differences has not been systematically explored. The spatial-frequency tuning of optic flow processing also has not been explored in a systematic manner. However, there is an unpublished study by Sekuler (Sekuler, 1991) that suggests that low spatial frequency information may be sufficient for accurate self-motion judgments. Speed-discrimination thresholds obtained with optic flow patterns blurred with a 5-diopter lens were similar to thresholds obtained with unblurred patterns. However, Sekuler did not test patterns where only the spatial frequency content and not the contrast was manipulated nor did she test patterns restricted to medium or high spatial frequencies.

In this study the ability to discriminate the direction of a curved motion path using optic flow patterns that were spatial-frequency

filtered was assessed. The results were compared to those obtained with spatially-filtered two-dimensional uniform (planar) motion.

Figure 8 shows the proportion correct responses plotted against center spatial frequency for the three subjects. Data points are the means across sessions, and the error bars represent the standard error of the mean. Proportion correct responses averaged over the three subjects are also shown by a thick solid line. As shown, for all subjects, performance varied in an inverted U-shaped manner as a function of center spatial frequency. Peak performance was achieved at a spatial frequency of 1.6 c/deg. At spatial frequencies of 0.4 and 9.6 c/deg, performance was decreased by about 25%, and at 0.2 c/deg performance dropped to chance level. These results indicate that some spatial frequencies are more effective than others in relaying information about self motion. Specifically, with the stimulus dimensions that we used motion information centered at 1.6 c/deg is the most effective spatial frequency range to achieve accurate path discrimination using optic flow patterns. When image spatial frequency is restricted to non-optimal bands, discrimination performance drops. Moreover, performance at this suprathreshold angular speed was comparable for the spatially-restricted and broadband stimuli; proportion correct response averaged

20 arcmin/sec
angular speed

KT
JHK
YL
average
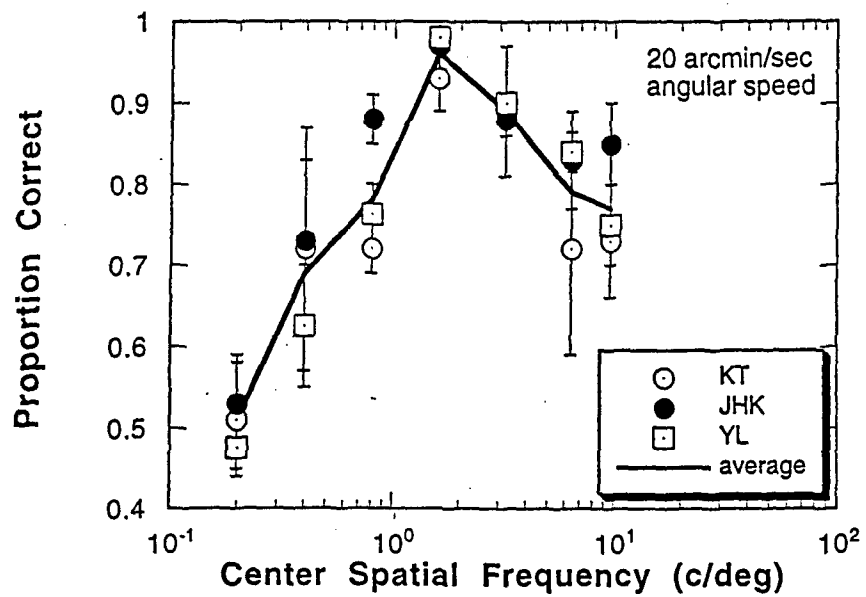
over the three subjects was 95.8% for the spatial-frequency restricted optic-flow patterns (1.6 c/deg center frequency) and 97.2% for the unfiltered patterns.

It was shown that a narrow band of spatial frequencies optimally placed was sufficient to achieve accurate path discrimination for suprathreshold levels of curvilinear motion. To determine whether the same narrow band of spatial frequencies is sufficient for observers to achieve the same path-discrimination thresholds as they did with the broadband stimuli, we measured proportion correct responses for path discrimination using optic flow patterns whose spatial frequency was restricted to 1.5 octaves centered at 1.6 c/deg. Judgments were made for six angular speeds, 2, 4, 8, 12, 16 and 20 min of arc/sec.

Figure 9 shows each subject's proportion-correct responses per angular speed. Path curvature is indicated on the upper x-axis. Data points represent the mean across sessions, and the error bars represent the standard error of the mean. The lines depict the best-fit Weibull functions to each subject's data. Closed symbols represent data obtained with the filtered patterns, and the open symbols represent data obtained with the unfiltered patterns. The dashed and solid lines depict the best-fit Weibull functions. The average angular speed threshold of the three

Curvature (10^-4 m^-1)
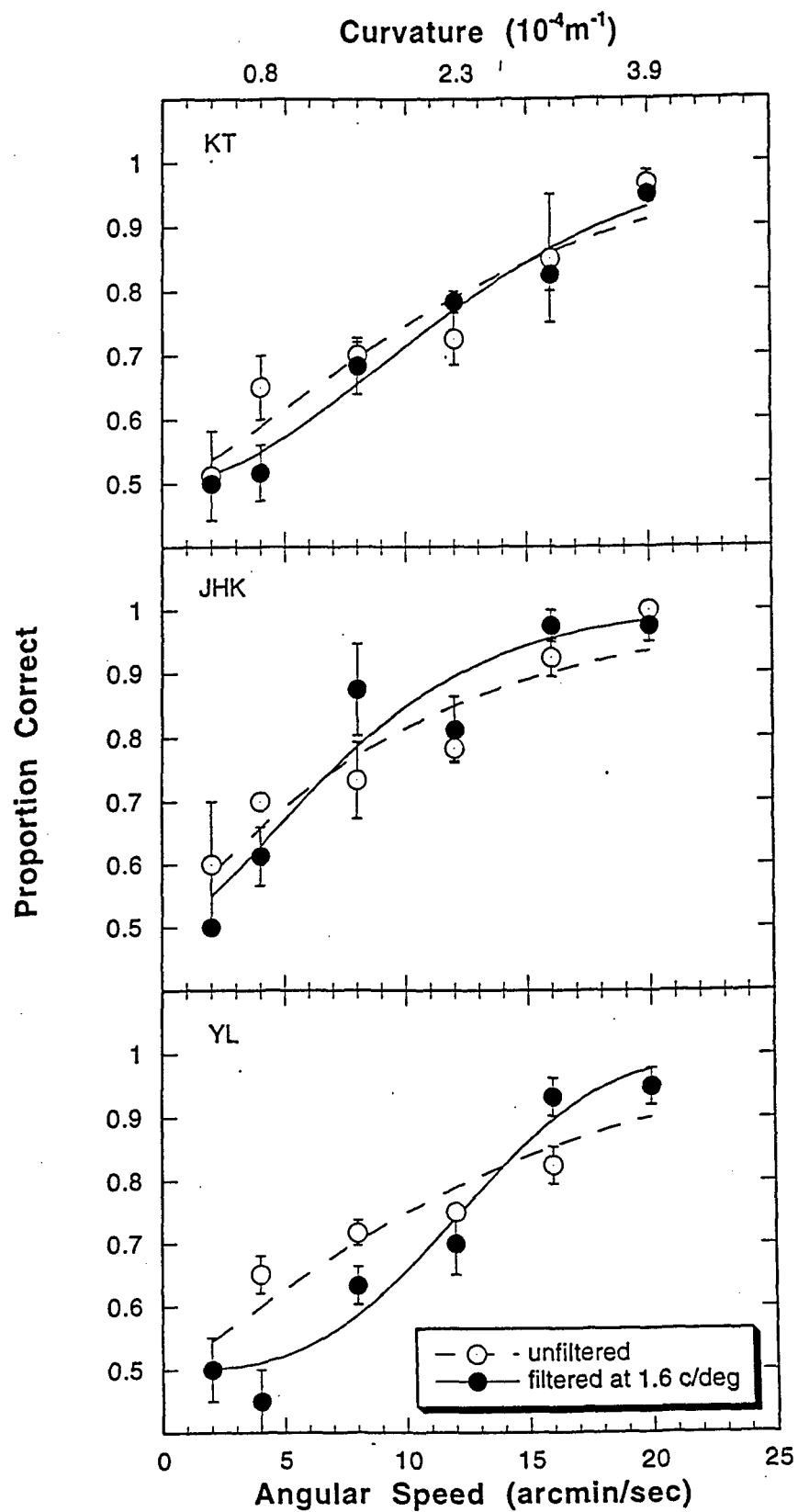
subjects, 12.0 min of arc/sec, is in close agreement with the average threshold obtained with the unfiltered patterns, 12.3 min of arc/sec. These results indicate that motion information carried by this narrow band of spatial frequencies is sufficient for observers to achieve the same path-discrimination thresholds as they did with the broadband stimuli. Performance did not suffer when the spatial frequency content of the optic flow patterns was restricted to a narrow band of frequencies centered at 1.6 c/deg.

Optimal spatial frequencies: Spatial tuning function of two-dimensional
uniform motion

Direction discrimination thresholds were measured using spatially
filtered patterns to determine the optimal spatial frequency range for
two-dimensional uniform (planar) motion. The results were then
compared to those obtained with the optic flow patterns. Proportion
"vertical" responses were measured for a suprathreshold test difference
of 5 deg for a range of center spatial frequencies. The planar motion
patterns were filtered with the same filters (excluding the lowest
spatial-frequency filter) and apparatus as used for the optic-flow
experiments. Judgments were made for six center frequencies (0.4, 0.8,
1.6, and 3.2, 6.4, and 9.6 c/deg). Each center frequency was presented 20
times in a random order, and each subject participated in a minimum of
two sessions.

Figure 10 shows the proportion correct responses plotted against
center spatial frequency for the three subjects. Data points are the
means across sessions, and the error bars represent the standard error of
the mean. The results are similar to the those obtained with the
optic-flow patterns; performance varied in an inverted U-shaped manner
as a function of center spatial frequency. Peak performance was achieved

at the same spatial frequency, 1.6 c/deg, as found for the optic-flow patterns. However, the tuning is somewhat narrower for the planar motion than was found with the optic-flow patterns. Furthermore, there is no loss in discrimination performance for a 5-deg direction difference when broadband stimuli are restricted to a narrow range of spatial frequencies centered at 1.6 c/deg. The following experiment examines threshold performance with spatially filtered planar motion patterns.

A narrow band of spatial frequencies optimally placed was sufficient to achieve accurate direction discrimination of planar motion when the direction difference was at a suprathreshold level, i.e. 5 deg. To determine whether the same narrow band of frequencies is sufficient for observers to achieve the direction-discrimination thresholds of the broadband stimuli, proportion correct responses for direction discrimination were measured using planar motion patterns whose spatial frequency was restricted to 1.5 octaves centered at 1.6 c/deg. Judgments were made for five relative test directions, 0, 1, 2, 3, and 5 deg. Each test direction was presented 20 times in a random order, yielding a total of 100 trials per experimental session. Each subject participated in a minimum of two experimental sessions.

Figure 11 shows each subject's proportion of "vertical" responses

Direction Difference (deg)

Proportion "Vertical" Judgments

KT

JHK

YL

- ○ - unfiltered
- ● - filtered at 1.6 c/deg
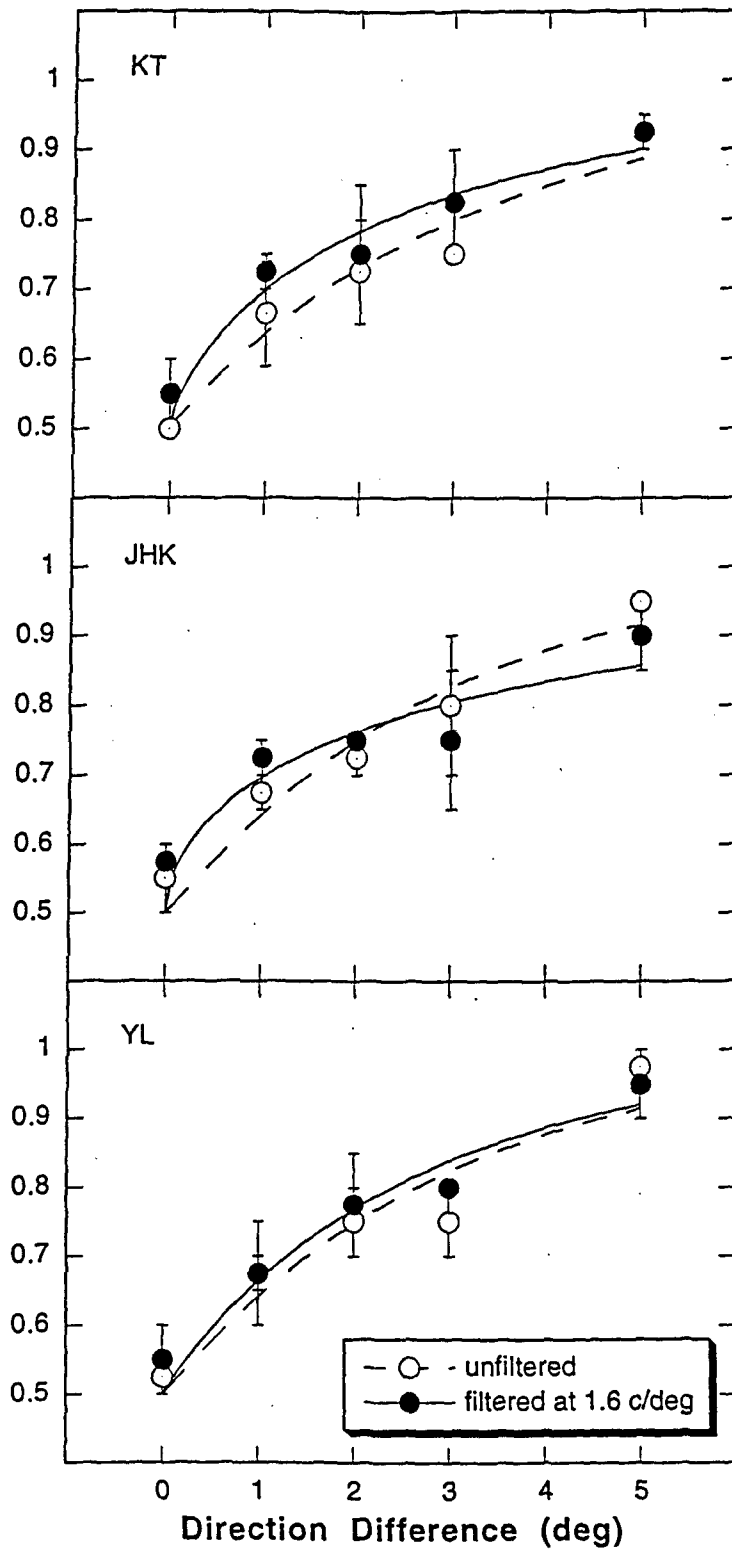
per relative test direction. Data points represent the mean across sessions, and the error bars represent the standard error of the mean. The lines depict the best-fit Weibull functions to each subject's data. Closed symbols represent data obtained with the filtered patterns, and the open symbols represent data obtained with the unfiltered patterns. The average direction-discrimination threshold of the three subjects is 2.7 deg which is similar to the 2.8-deg threshold obtained with the unfiltered patterns. These results indicate that motion information carried by this narrow band of spatial frequencies is sufficient for observers to achieve the same direction-discrimination thresholds as they did with the broadband stimuli. Performance did not suffer when the spatial frequency content of the planar motion patterns was restricted to a narrow band of frequencies centered at 1.6 c/deg. Not only is the peak center frequency, i.e. 1.6 c/deg, the same for the direction discrimination of the planar motion and optic flow patterns but for both types of motion, there is no loss in performance due to a optimally-placed, narrow spatial frequency band.

A current hypothesis is that the directionally-selective mechanisms that underlie the perception of planar motion also underlie the perception of optic flow (Lappe & Rauschecker, 1993; Perrone, 1992; Perrone &

Stone, 1994; Warren & Saunders, 1995). This hypothesis derives from the view that the physiological mechanisms underlying the perception of two-dimensional and three-dimensional motion are found in areas MT and MST and from several neurophysiological findings. Neurons in the directionally-sensitive striate cortex project directly to the middle temporal (MT) area of the superior temporal sulcus. MT neurons, in turn, project to the medial superior temporal (MST) area of the superior temporal sulcus which also has a high proportion of directionally selective cells. Neurons in area MT respond to translation in the fronto-parallel plane (Tanaka, Hikosaka, Saito, Yukie, Fukada, & Iwai, 1986), whereas many MST neurons respond selectively to planar and radial stimuli with some responding to combinations of planar and radial and circular stimuli (i.e. optic flow structure) (Duffy & Wurtz, 1991a; Orban, Laae, Verri, Raiguel, Xiao, Maes, et al., 1992; Saito, Yukie, Tanaka, Hikosaka, Fukada, & Iwai, 1986; Tanaka, Fukada, & Saito, 1989; Tanaka & Saito, 1989). Indeed, Duffy and Wurtz (1991b) have suggested that selectivity for complex motion, such as optic flow, can be accomplished by planar response gradients varying in their strength, directional preference, and degree of overlap (Duffy & Wurtz, 1991b). Likewise, Verri and colleagues (Verri, Straforini, & Torre, 1992) have modelled

MST neuronal responses using linear integration from an appropriately organized set of MT input units. Our finding that the peaks of the spatial-frequency tuning functions (1.6 c/deg), and their general shapes, were the same for both optic flow and planar motion lends support to the hypothesis that there is a common underlying motion processing mechanism(s).

The peak spatial frequency for direction discrimination of the optic flow patterns and the planar motion was the same, 1.6 c/deg, but the tuning function for the optic flow patterns was slightly wider than the function for the planar motion. The fact that, for the optic flow patterns, performance remained above chance level for higher spatial frequencies than for the planar motion is most likely due to the presence of low velocities in the retinal image of the optic flow patterns. The peak of the contrast modulation transfer function shifts to higher spatial frequencies as the velocity decreases. It could be that for the optic flow patterns, the low velocities present in the retinal images recruited mechanisms with peaks located at higher spatial frequencies. We predict that as the mean retinal speed of optic flow patterns increases, the peak of the spatial-frequency tuning function will decrease.

Characteristics of the spatial tuning function: Optic Flow[7]

One cannot infer from the previous study whether the critical factor determining the spatial frequency tuning function for direction discrimination of optic flow is defined in terms of object or retinal spatial frequency. Spatial frequency tuning functions were measured by varying the center spatial frequency of filtered optic flow images and determining direction discriminability at a constant viewing distance. This method inherently confounds the object and retinal spatial frequencies defining the spatial frequency tuning functions. The question of whether the critical dimension is defined in object or retinal units has been asked of various other tasks such as spatial-frequency discrimination, velocity discrimination, letter identification, and reading rate (Burbeck, 1987; McKee & Welch, 1989; Parish & Sperling, 1991; Legge, Pelli, Rubin & Schleske, 1985). The results of these studies do not converge on a single answer. Object spatial frequency appears to be the defining dimension for spatial frequency discrimination, letter identification, and reading rate (Burbeck, 1987; Parish & Sperling, 1991; Legge, Pelli, Rubin & Schleske, 1985), whereas velocity discrimination is better defined in retinal units (McKee & Welch, 1989).

To determine whether the optimal spatial frequency range for path

discrimination is defined in object or retinal dimensions, object and retinal spatial frequencies were varied independently (cf. Parish & Sperling, 1991). Object spatial frequency was manipulated by varying the center spatial frequency of the filtered optic flow images, and retinal spatial frequency was manipulated by varying viewing distance, keeping the retinal image size constant. Proportion correct responses were collected for a range of center spatial frequencies. Angular speed was set at a constant factor above the baseline threshold, chosen arbitrarily to be approximately 1.6 times threshold. If object spatial frequency is the determining factor for path-discrimination, there should be no shift in the optimal spatial frequency range across the different viewing distances.

Figure 12 shows the proportion of correct responses for the three subjects plotted against center spatial frequency in terms of object (left panel) and retinal (right panel) spatial frequency. Data points are the means across sessions, and the error bars represent the range of response. As shown, performance varied in an inverted U-shaped manner as a function of center spatial frequency. This pattern of results replicates the previous finding of Kim & Turano (1996). The drop in performance at the higher spatial frequencies is in agreement with the
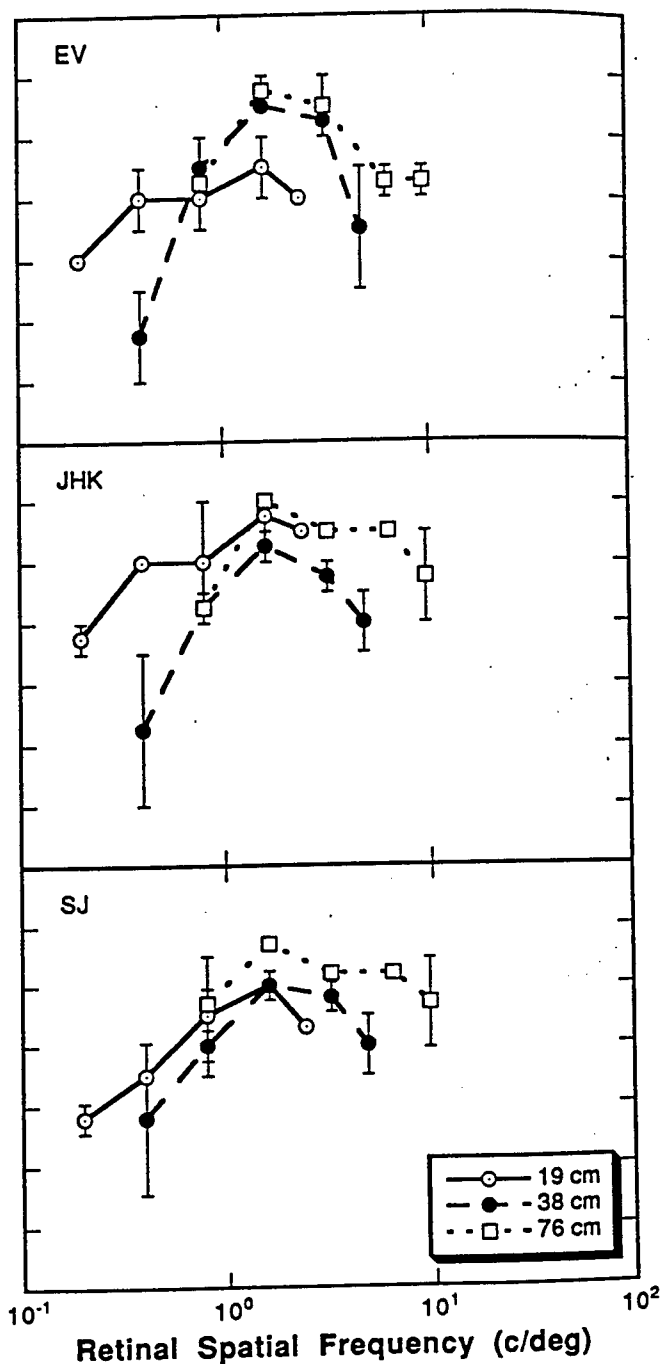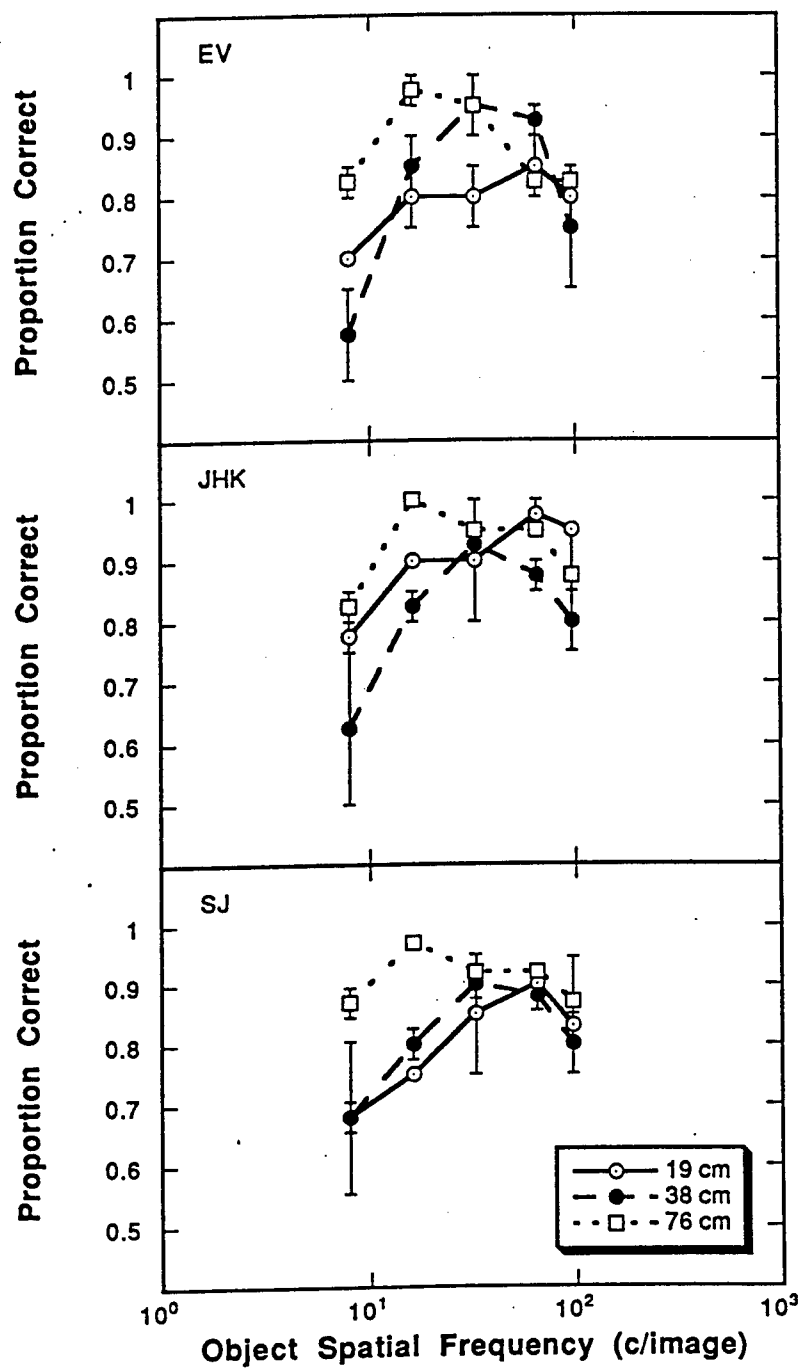
widely accepted notion that the motion system is less sensitive to high spatial frequency information (Pantle, 1978; Cavanagh, Boeglin, & Favreau, 1985; Cleary & Braddick, 1990). For all subjects, peak performance was achieved at different object spatial frequencies (16, 32, and 64 c/image) but always at the same retinal spatial frequency (1.6 c/deg) for the viewing distances of 76, 38, and 19 cm. These results demonstrate that it is the retinal spatial frequency, and not the object spatial frequency, that governs performance for path discrimination.

Another question addressed in this study is whether the observed optimal spatial frequency range is constant across various optic flow speeds. Previous studies using sinusoidal gratings as stimuli have examined the spatial frequency tuning of directionally selective mechanisms. The results have shown that the peak of the spatial frequency tuning function varies inversely with stimulus speed (Kelly, 1979; Wilson, 1985). Given the generally accepted assumption that the directionally-selective mechanisms also underlie the perception of optic flow (Heeger, 1987; Lappe & Rauschecker, 1993; Perrone, 1992; Perrone & Stone, 1994; Warren & Saunders, 1995; Kim & Turano, 1996), it may be that the peak of the spatial frequency tuning function of optic flow patterns will vary similarly. On the other hand, optic flow generates

multiple image speeds. Image motion of each element in the optic flow patterns is dependent on the simulated angular and forward speeds of the observer as well as on the position of each element within the simulated environment. The image speed of each texture element is inversely related to its distance in depth from the observer. Given that optic flow patterns contain a range of image speeds, the tuning function may vary in a different manner with speed than that obtained with gratings. In the previous study, spatial frequency tuning functions were measured for path discrimination and for direction discrimination of two-dimensional uniform motion. The tuning function for the optic flow patterns was slightly wider than the function for the uniform motion. One possible explanation for this observation is that the many velocities present in the image of the optic flow patterns recruited additional mechanisms with peaks located at nearby spatial frequencies, thereby yielding a wider tuning function. Thus, it may be that the tuning function will vary in its bandwidth, but not in its peak as the image speed of the optic flow patterns varies. In order to examine the interaction of spatial frequency and speed of optic flow patterns in path discrimination, the mean image speed of optic flow patterns was varied by manipulating the simulated forward speed (cf. Turano & Wang, 1994).

To examine whether optic flow speed affects the optimal spatial frequency range for path discrimination, path discrimination was measured using spatially filtered optic flow patterns at various optic flow speeds. Proportion of correct responses were determined for mean image speeds of 0.6 and 9.0 deg/sec (forward speeds of 5 and 26 m/sec). Angular speed was set at a constant factor above threshold, chosen arbitrarily to be approximately 1.6 times threshold.

Figure 13 shows the mean proportion correct for the three subjects plotted against the center spatial frequency at the slow (mean image speed of 0.6 deg/sec), intermediate (mean image speed of 2.3 deg/sec) and fast (mean image speed of 9.0 deg/sec) speeds (5, 15, and 26 m/sec forward speeds respectively). The error bars represent $\pm$ 1 standard deviation.

For the two fastest speeds, performance varied in an inverted U-shaped manner as a function of center spatial frequency. However, the spatial frequency tuning function shifted as a function of optic flow speed. As the speed increased, the peak of the tuning function shifted toward lower spatial frequencies. A shift by a factor of approximately two produces a relatively good superposition of the two curves (the exception being the data points at 4.8 c/deg). Peak performance deg for

average

Image speed (Forward speed)
— 0.6 deg/sec (5 m/sec)
⊙ 2.3 deg/sec (15 m/sec)
▢ 9.0 deg/sec (26 m/sec)

Proportion Correct

Center Spatial Frequency (c/deg)
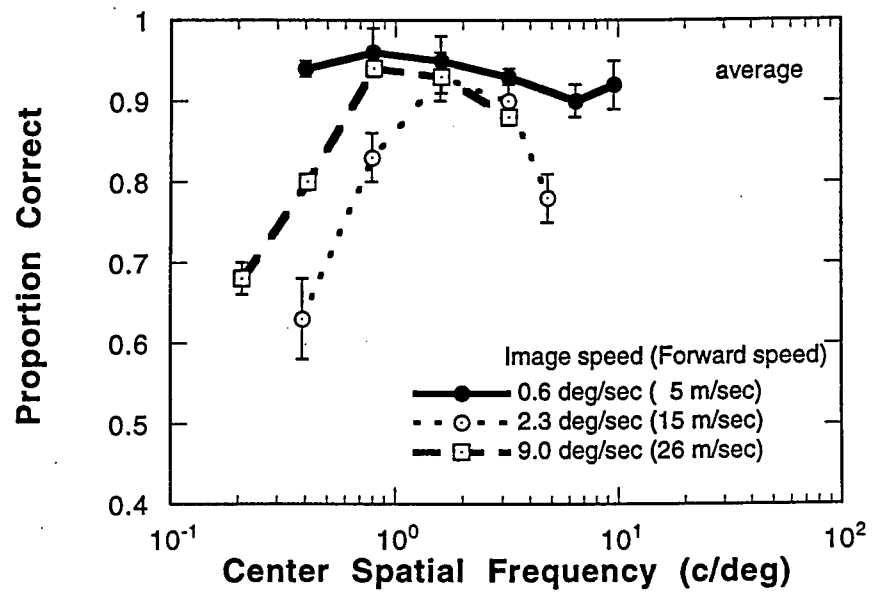
the 2.3 deg/sec speed was obtained at the center spatial frequency of 1.6

c/ and for the 9.0 deg/sec speed the peak was at 0.8 c/deg. This shift in

the spatial frequency tuning with increasing optic flow speed is similar

to the previously reported finding with sinusoidal gratings (Kelly, 1979;

Wilson, 1985). In Kelly's study, the peak of the contrast sensitivity

function for the detection of a grating moving at 3 deg/sec was 1.5 c/deg.

The peak shifted to 0.5 c/deg for a grating moving at 11 deg/sec. The

magnitude of shift is comparable to what we observed with the optic

flow patterns. The similarity between the spatial characteristic of the

motion mechanisms underlying sinusoidal grating motion

(one-dimensional motion) and optic flow (three-dimensional motion) adds

support to the hypothesis that the same direction selective mechanisms

constrain performance with the two classes of stimuli.

At the slowest speed tested, a different pattern of response was

obtained. The tuning function remained fairly flat across the range of

spatial frequencies tested. Performance was higher with the slowest

optic flow pattern at the non-optimal spatial frequencies compared to

performance with the faster optic flow patterns. Subjects reported that

they sometimes perceived the dots in the optic flow patterns change

their positions across the frames instead of perceiving smooth motion at

the slow image speed. It is generally hard to discern the positions of dots filtered at low center spatial frequencies because of their blurred images. However, at slow speeds, it is possible to locate the positions of dots as the blurred images appear to have some rigid features. Nakayama and Tyler claim that for moving elements with recognizable position cues and small distances in position, position sensitivity dominates to determine the detection threshold (Nakayama & Tyler, 1981). It may be, then, that the position information from the slowest optic flow patterns enabled the subjects to determine the path directions.

CHAPTER IV

GENERAL DISCUSSION

As an initial step in our endeavor to understand the role of vision in self-motion perception, the effects of eye movements on motion perception were investigated. This topic has been largely unexplored, yet it is critical for understanding self-motion perception as well as for developing motion-perception models. Most models of motion perception do not take into account the fact that eye movements alter the retinal-image motion which feeds into an image-motion processor. Moreover, it was previously unknown whether the effects of eye movements could be accounted for by considering only the changes in the retinal-image motion.

The results of one study (Turano,1995) showed that when subjects viewed optic-flow patterns under conditions of image stabilization (to minimize the retinal effects of eye movements) subjects required more of an angular deviation to discriminate a circular from a straight motion path than they did with unstabilized viewing. Analyzing the results in terms of retinal-image motion revealed that performance could be explained on the basis of retinal motion alone. Eye movements may have served to boost the retinal speed to stimulate visual motion sensors. This explanation is plausible given the findings of a second study in which the

smallest detectable speed difference between sinusoidal gratings was measured under normal and stabilized viewing conditions (Heidenreich & Turano,1996). In that study, speed discrimination thresholds, expressed as Weber ratios relative to stimulus speed, were higher when measured with image stabilization than when measured under normal viewing conditions for slow stimulus speeds. When equated in terms of retinal speed, there was no difference between the stabilized viewing and the normal viewing thresholds. The two studies, taken together, suggest that the motion was too slow to stimulate the motion sensors in the stabilized viewing condition.

In another study (Turano & Heidenreich, 1996), subjects judged speed differences of sine-wave gratings while they simultaneously pursued a separately moving bar. For conditions where the eye moved at a slower speed than the gratings, regardless of whether the eye moved in the same or opposite direction, the results could be explained on the basis of retinal motion alone. But when the eye moved at a faster speed than the grating, in the same direction, performance was significantly lower than predicted by retinal motion. Under these conditions, it may be that an extra-retinal signal (conveying information about the eye movement) interferes with the retinal-motion signals when judging the

speed of distal stimuli that are not pursued.

A fourth (Turano & Heidenreich, submitted for publication in <u>Vision Research</u>) and fifth study (Turano, 1996) focussed on subjects' ability to use extra-retinal information to recover distal stimuli motion, in essence, to discount the retinal-image effects of eye movements. Subjects made speed matches (and direction matches) between two successively-presented gratings (or dot patterns) as eye movements were monitored. Subjects fixated a central stationary point during the presentation of the standard grating (or dot pattern), and subjects tracked a drifting bar superimposed on a test grating (or dot pattern) in the other interval. Subjects judged which grating (or dot pattern) moved faster (or more vertical). The results showed that subjects could accurately match the speed (or direction) of the standard stimulus with the test stimulus even when the eyes move in the opposite direction to the test stimulus. In that regime, subjects appear to use extraretinal information to discount the retinal effects of eye movements to make speed judgments about distal stimuli. However, when the eyes move in the same direction as the test stumulus but at a slower speed, subjects fail to accurately match the standard stimulus to the test stimulus. In that regime, subjects match the retinal motion of the standard and test

stimuli. It appears that subjects cannot use extraretinal information to discount the retinal effects of eye movements to make speed (or direction) judgments about distal stimuli.

The retinal-image velocity appears to be an important factor governing whether eye movements affect motion judgments. In general, for retinal-image speeds faster than 1.5 deg/s, eye movements do not affect judgements of distal motion. However, for retinal-image speeds slower than 1.5 deg/s, eye movements affect distal motion judgments.

The results of these studies have potential applications to AF and civilian technology challenges. In operations of aircraft control or target acquisition the failure to perceive small speed or direction differences could produce serious errors in the pilots' performance. Up to now little has been known about the effects of eye movements on the ability to perceive small speed or direction differences. These results indicate that the most precise speed differences are obtained when eye movements are minimized. Thus in situations of artificial or image-controlled environments, speed or direction judgments can be optimized by providing stationary fixation marks to the observers. With regard to estimations of distal motion, eye movements had little effect when the retinal motion was faster than 2 deg/sec. At slower speeds, eye movements do affect

our perception of distal motion; perceived speed is underestimated.

In a separate set of experiments directed at understanding the role of vision in self-motion perception, the spatial frequency requirement for the perception of motion direction was determined.

The results of one study (Kim & Turano, submitted for publication in Vision Research) demonstrated that there is a band of spatial frequencies that is optimal for accurate path discrimination. The same band of optimal frequencies was shown to be optimal for direction discrimination of two-dimensional uniform motion, supporting the view that the same processing mechanism underlies the perception of the two classes of stimuli. Furthermore, the results of the study showed that a narrow band of the optimal spatial frequencies is sufficient for accurate judgments of motion direction. Performance did not suffer when the spatial frequency content of the motion patterns was restricted to a narrow band of optimal frequencies.

The results of this study have potential engineering applications. The current trend in simulations (e.g. flight simulators) is to reproduce the real-world scene with high fidelity. The same principle is true for remote sensing devices or helmet-mounted displays where images are transmitted. Yet the transmission of high-fidelity images is costly. It

may be that high fidelity is not necessary for accurate performance; information in the various spatial frequencies may not be equally effective for the task at hand. Our study showed that for direction discrimination with optic flow or planar motion, performance was not equivalent across all spatial frequencies. Information in some of the spatial frequencies was incapable of producing above chance discrimination performance. Given that a narrow band of spatial frequencies, optimally placed, is sufficient to support path-discrimination performance indicates that we can increase transmission efficiency without a performance penalty. It may be possible to filter images of real-world scenes and transmit the information contained only in those spatial frequencies that are effective for successful path-discrimination performance. The reduced bandwidth for the transmitted information would translate into a savings in time without a cost in performance.

An additional study (Kim & Turano, submitted for publication in Perception) was conducted to explore the general nature of the spatial frequency tuning function. This is an important study from both a basic science perspective--to reveal the operating characteristics of the underlying motion mechanism-- and an applied science perspective--to

reveal the filtering parameters necessary to achieve optimal performance. The results revealed that the critical spatial frequency dimension is not invariant across viewing conditions. That is, optimal performance is achieved for images filtered in cycles per degree of visual angle, not cycles per image. The study also showed that the optimal spatial frequency range shifts to lower values with increasing optic flow speed. From a practical standpoint, this lack of invariance is unfortunate. However, with estimates of probable flow speeds and viewing distance, calculations can be made of the appropriate spatial frequency filter parameters which will optimize performance.

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ENDNOTES

1. Excerpts taken from Heidenreich, S.M. and Turano, K. (1996) Speed discrimination under stabilized and normal viewing conditions. Vision Research, 36, 1819-1825.

2. Excerpts taken from Turano, K. (1995) Self-motion path discrimination: Effects of image stabilization. Journal of Vestibular Research, 5, 411-420.

3. Excerpts taken from Turano, K. and Heidenreich, S.M. (1996) Speed discrimination of distal stimuli during smooth pursuit eye motion. Vision Research, 36, 3507-3517.

4. Excerpts taken from Turano, K. A. and Heidenreich, S.M. Eye movements can affect the perceived speed of visual motion. Submitted for publication in Vision Research.

5. Excerpts taken from Turano, K.A. (1996) Asymmetric effects of eye movements in motion perception. Investigative Ophthalmology & Visual Science (Suppl.), 37, S467.

6. Excerpts taken from Kim, J. and Turano, K.A. Optimal spatial frequencies for direction discrimination of optic flow and planar motion. Submitted for publication in Vision Research.

7. Excerpts taken from Kim, J. and Turano, K.A. Characteristics of the spatial tuning function for path discrimination of optic flow. Submitted for publication in Perception.

Appendix 1
Personnel supported and/or associated with effort.

Kathleen A. Turano   Principal Investigator

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Appendix 2

Publications stemming from the research effort.

Journal Articles

Turano, K. A. and Heidenreich, S.M. Eye movements can affect the perceived speed of visual motion. Submitted for publication in <u>Vision Research</u>.

Kim, J. and Turano, K.A. Optimal spatial frequencies for direction discrimination of optic flow and planar motion. Submitted for publication in <u>Vision Research</u>.

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Appendix 2 (continued)

Turano, K. (1995) Self-motion path discrimination: Effects of image stabilization. <u>Journal of Vestibular Research</u>, <u>5</u>, 411-420.

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Published Abstracts

Kim, J and Turano, K.A. (1997) Invariance of optimal spatial frequencies for direction discrimination of optic flow paths. <u>Investigative Ophthalmology & Visual Science (Suppl.)</u>, 38.

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Appendix 2 (continued)

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